

RESPONSES OF *EUCALYPTUS CAMALDULENSIS* SPROUTS TO SHADE: AN EVALUATION OF CANOPY PLASTICITY

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SUMMARY

Eucalyptus spp. is the main tree used in cellulose production worldwide, cultivated mostly in extensive monocrop plantations. However, due to concerns on environmental impacts, fear on decrease of food production related to the size of cultivated area, its location near human settlements with few jobs generation, eucalypt cultivation is no longer encouraged in many places. At the same time, large plantations hold the opportunity to integrate eucalypt into agroforestry systems (AFS) in a variety of production systems with many social, economical and environmental advantages. In this study we studied canopy modifications of *E. camaldulensis* sprouts under different degrees of shade. The plants were located on a gradient of available solar irradiation ranging from 51 to 94%. *E. camaldulensis* showed canopy plasticity with modified radiation interception patterns under diverse irradiances. Most of these variations were of small amplitude with some important variables remaining almost unchanged (leaf density, canopy percentage, tree, trunk and canopy height) or increasing only slightly (leaf area index and canopy opening). The main changes presented by *E. camaldulensis*, with a steep increase towards full sun, were: foliage area, canopy surface, canopy volume and area of canopy projection. In order to design appropriate agroforestry systems with young eucalypt growing under the shade of other crops, it is necessary to determine at which point the observed variable changes can support reasonable production.

INTRODUCTION

Eucalyptus spp. is the principal tree used in cellulose production and is cultivated worldwide, mainly in monocrop plantations (Couto and Dubè, 2001). Well adapted to the soil and climatic conditions of Brazil, eucalypts today occupy about 4.9 million hectares, representing 67% of the planted forests in Brazil (ABRAF, 2012). Despite this, Brazilian native forests still provided 62% of all timber wood in 2006, reflecting the difficulties for farmers to make long-term investments in the prevalent (monocrop) production system. However, due to the size of cultivated area near densely populated

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areas with few jobs generation, eucalypt cultivation is no longer encouraged in many Brazilian States. Also, it is not considered socially friendly due to a lack of jobs and production output generated in the country. An alternative production method that diminishes the necessity of long-term investment and at the same time generates both jobs and products is to integrate eucalypt into agroforestry systems (AFS) (Lunz and Franke, 1998; Tsukamoto Filho, 1999). To this effect, the use of eucalypt in AFS is evolving and diversifying (Macedo *et al.*, 2010). Despite good development in some AFS, such as in agrisilviculturals and silvipastorals, there still is a lack of knowledge of eucalypt responses to environmental modifications.

The implementation of AFS is one way to maximise the benefit of interactions and better use of available resources. AFS can be advantageous in many aspects – *i.e.* short-term investment revenue, rising productivity, soil melioration, etc. Plants show many different responses to environmental modification. Most eco-physiological aspects involved in interactions between species are not well understood. Understanding resource capture is necessary to design appropriate AFS that maximises beneficial interactions. Most of the studies dealing with plant structure and radiation interception were carried out in the 1950s–1980s (Alvim and Kozlowski, 1977; Monsi and Saeki, 1953; Monteith, 1965 and 1972). For a long time, the importance of plant responses and adaptation to their environment was neglected since many studies were designed to analyse productivity only in homogeneous stands.

The main drivers of growth and yield of plant communities are solar radiation and the attenuation patterns found when water and nutrients are available (Ong *et al.*, 1996; Righi and Bernardes, 1999). Plant temperature varies with incident irradiation, transpiration, convection and thermal conduction (Gates, 1965). Linacre (1964), studying different cultures, concluded that air and leaf temperature were equivalent at ~ 33 °C. Below that, leaf temperature is warmer than air and above that, leaves tend to be colder. Direct exposure of leaves to solar radiation rises their temperature, thus intensifying differences in vapour pressure between the foliar mesophyll cells and the air. This results in high transpiration rates, which have a thermoregulatory function (Sutcliffe, 1980). High irradiance levels normally found in the tropics may damage the photosynthetic system, particularly for shade-adapted leaves or leaves in which the photosynthetic metabolism has been inhibited by other stressors such as extreme temperatures or water deficiency (Jones, 1994).

Hallé and Oldman (1970) were pioneers in describing the periodic development of the shoot systems of various tree species under natural conditions in tropical areas. The canopy structure is important by defining branches and leaves distribution that directly influences the interception and use of solar radiation. Photosynthetic efficiency depends on the photosynthesis per unit leaf area and the way solar radiation is intercepted by the plants (Campbell and Norman, 1989), leading to a specific capacity for growth and productivity. Leaf area index (LAI) and leaf longevity are the most important factors defining dry matter production that results in growth and yield (Bernardes *et al.*, 1996). With canopy development, not only micro-environmental conditions are changed, but also plant arrangement, leaf age and the distribution of photoassimilated compounds within its structure. These modifications alter the

way radiation is intercepted and used by plants. Therefore, plants need strategies sustainable over a series of generations, which can deal successfully with a variety of environments, landscapes, competing species and disturbances (Westoby, 1998).

More recently, the adequacy of *Eucalyptus*-based agroforestry systems has been subject of studies (Couto *et al.*, 1994; Dubè *et al.*, 2002; Prasad *et al.*, 2010). The intercrop of annuals crops and trees allows for a fast amortisation of at least part of the establishment costs, a reduction of risks and an improved use of natural resources (Dubè *et al.*, 2002; Garrity and Marcado, 1994; Huxley, 1999).

The physiological aspects involved in the interaction between two or more species are very complex and further research is needed to fully understand them. Improved knowledge of resource capture and use by an AFS will lead to a more appropriate cultivation design with spatial and temporal management. To this end, we hypothesise that *Eucalyptus* shows architectural modifications when cultivated in diverse environments. Therefore, a trial was performed to verify the canopy modifications of *Eucalyptus camaldulensis* sprouts in response to a shade gradient.

MATERIAL AND METHODS

The trial was conducted in 2011 at the Experimental Station of Forestry Science of Anhembi (ESFSA), Department of Forestry Science of the Escola Superior de Agricultura “Luiz de Queiroz”, University of São Paulo (ESALQ/USP) in Anhembi-SP/Brazil (22°40'S, 48°10'W – altitude 455 m). Mean air temperature is 23 °C with an annual precipitation of 1100 mm (climate classification of Cwa type according to Köppen). The studied area, located on a flat slope, is an Oxisol typically yellow-red with a moderate A-horizon and sand-texture.

Eucalypts were planted in February, 1998 with a 3 × 2 m spacing between trees and were cut down in 2007. Thus, the sprouts at the time of this study were four years old. The only management procedure after harvesting the trees in 2007 was an annual treatment against ants. Fertilisers were not applied between 2007 and 2011. The sprouts were not thinned with stumps presenting different number of trunks. The values measured for all sprouts on one tree stump were combined to represent one tree, *i.e.* canopy height averages the values for all sprouts on one stump; canopy volume was the sum of the individuals on one stump; etc. The study area has a shade gradient due to the presence of *Eucalyptus urophylla* planted in the adjacent block on the other side of the road (10.2 m width) (Figure 1).

The influence of shade on *E. camaldulensis* was measured in a transect of 11 distances (10.2; 13.2; 16.2; 19.2; 22.2; 25.2; 28.2; 34.2; 43.2; 55.2 and 88.2 m) from the shading trees (*E. urophylla*) with 3 replicates per distance. Tree and trunk height and canopy diameter were directly measured by cutting the trees at the soil level. Tree height was defined as the distance from the soil level to the highest point of the canopy and trunk height as the distance from the soil level to the insertion of the lowest branch. Trees were cut down at the soil level and the entire plant was weighed at field by using a 300 kg capacity scale (Pesola® brand) in order to obtain the wet total above ground biomass. All leaves were removed and weighed in the field using a precision spring

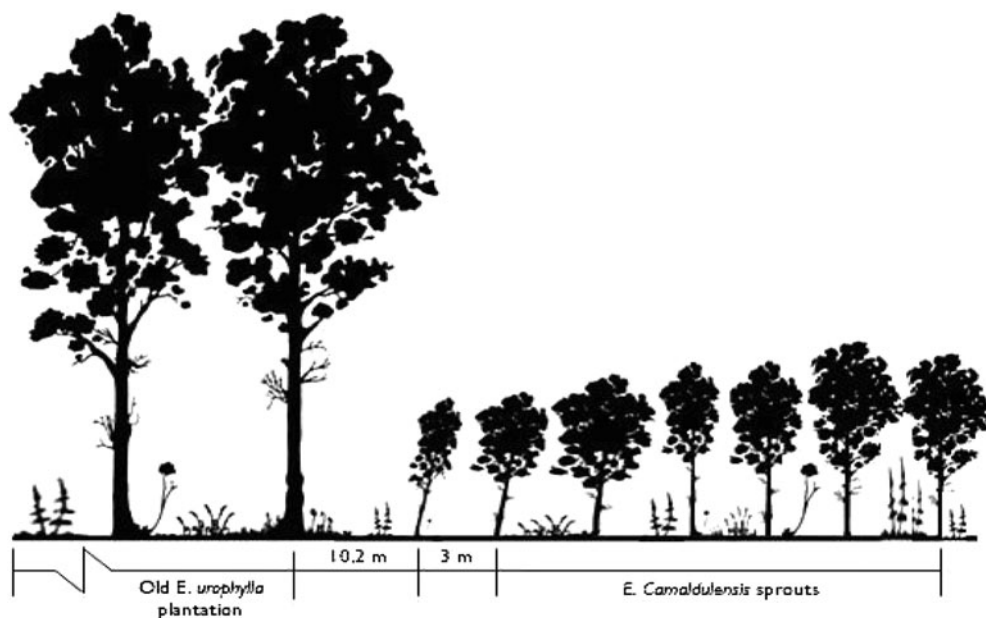


Figure 1. Schematic drawing of a cross-section of the experimental field at the Experimental Station of Forestry Science of Anhembi (ESFSA) belonging to the Department of Forestry Science of the Escola Superior de Agricultura “Luiz de Queiroz”, University of São Paulo (ESALQ/USP) in Anhembi-SP/Brazil (22°40’S, 48°10’W) showing the distribution of shading trees (*E. urophylla*) and sprouts of *E. camaldulensis*, both of which were planted with a spacing of 3x2m. Drawing not to scale.

balance (Pesola[®] brand). Samples were taken from the entire plant and then after weighing placed in paper bags and tagged. Leaf areas of the samples were measured at the laboratory using an area meter Li-3100 (Li-Cor Inc.). The samples were dried in a forced-air oven at 65 °C until they reached constant weight. Total leaf areas and total dry biomass were then determined by calculation.

Specific leaf area (SLA), which can be used to infer leaf thickness (*for more details on the methodology for leaf thickness estimation, please refer to Vile et al., 2005*), varies according to light intensity and may serve as an indicator of plant adaptation to a particular environment. SLA ($\text{m}^2 \cdot \text{kg}^{-1}$) of *E. camaldulensis* was calculated by dividing leaf area by dry mass of leaves for each evaluated distance from the shading trees.

Canopy characteristics were evaluated according to the methodology proposed by Leong (1980): (i) canopy height (the difference between tree and trunk heights); (ii) canopy percentage (canopy height divided by tree height multiplied by 100); (iii) canopy opening (average canopy diameter divided by tree height multiplied by 100); (iv) canopy filling rate (the quotient between the diameter average and the canopy height, which indicates the canopy rounding off); (v) canopy projection (canopy diameter average divided by trunk diameter multiplied by 100); (vi) canopy volume, calculated considering a conical shape; (vii) canopy surface, calculated considering the same conical shape; and (viii) leaf density (the quotient between the total leaf area and canopy volume).

Available solar irradiation (IR%) was estimated according to the model proposed by Bernardes *et al.* (1998) adapted from Goudriaan (1977) with tree heights, distances between trees and canopy width (equation 1) were taken into consideration.

$$IR = \frac{I}{I_0} = \frac{1}{2} \left\{ \sin \left(\arctan \left(\frac{d - \frac{C_w^2}{d}}{H_r} \right) + D \right) + 1 \right\} \quad (1)$$

where I = daily radiation ($\text{MJ}\cdot\text{m}^{-2}$) that reaches the canopy of the intercalary crop; d = distance from the row of shading trees (m); I_0 = daily radiation ($\text{MJ}\cdot\text{m}^{-2}$) on a horizontal surface above the tree canopy; C_w = tree canopy radius (m); D = declivity of the ground (radians); H_r = relative tree height (m), obtained by equation 2:

$$H_r = H_a - H_{ci} \quad (2)$$

where H_a = tree height (m); H_{ci} = height of intercalary crop (m).

Shading tree characteristics (height and canopy radius) were measured with a dendrometric rule and directly with a measuring tape.

A regression analysis on the relationship between irradiation fraction, tree canopy variables and leaf area was carried out. Several models were tested and the best model was selected for each pair of variables. In order to select the best model, residual analysis was used as the most important criterion. Other parameters used for model statistics were the coefficient of determination and the significance of the F and t tests.

RESULTS

Shading trees had an average height of 42 m with a canopy radius of 6.8 m in the direction of the experimental field with *E. camaldulensis*. The estimated radiation reaching the top of the *E. camaldulensis* trees (details in Table 1) ranged from 51 to 94% at the evaluated distances from the shading trees (between 10.2 and 88.2 m).

Canopy data are listed in Table 1. Canopy diameter increased with available irradiance. Canopies were smallest at the shadiest location (51% IR) with a diameter of only 1.76 m. In the least shady location, plants growing at 94% IR had a canopy diameter of 5.4 m. This variable was more responsive to irradiance levels up to about 70% IR and tended to stabilise with further irradiance increments. Likewise, the soil covered by the canopy depended on irradiance levels: plants in a shadier location (51% IR) occupied only 1.8 m², while trees in the next location (58% IR) occupied 3.3 m². In sunnier places, canopy cover was more than twice this area (7.2 m²).

Canopy volume and surface augmented steadily with the increase of solar irradiation with a small increment in canopy opening of no statistical significance. Canopy volume varied from 2.5 m³ to almost 16 m³ from the shadiest position (51% IR) to the most illuminated position (94% IR). Canopy surface varied notably, with trees in the shadiest position presenting only a fifth part (11.7 m²) of those presented by trees located in almost full sun (56 m²). Canopy projection (canopy diameter divided by trunk diameter expressed in percentage) did not show any significant tendency with increasing availability of solar irradiation (Table 1).

Table 1. Parameters evaluated (means and standard deviations) of *Eucalyptus camaldulensis* sprouts in a shade gradient in the experimental field at the Experimental Station of Forestry Science of Anhembi (ESFSA), Department of Forestry Science of the Escola Superior de Agricultura “Luiz de Queiroz”, University of São Paulo (ESALQ/USP) in Anhembi-SP/Brazil (22°40’S, 48°10’W). Equations that describe the relationship of parameters with irradiation level are shown below as well their coefficient (R^2) and significance level.

Distance (m)	Solar radiation (%)	Canopy diameter (m)	Canopy height (m)	Canopy surface (m ²)	Canopy volume (m ³)	Area of canopy projection (m ²)	Canopy rounding off	Canopy opening (%)	Canopy percentage (%)	Canopy projection (%)	Specific leaf Area (m ² .kg ⁻¹)	Leaf density (m ² .m ⁻³)	Leaf area (m ²)	LAI (m ² .m ⁻²)	Total dry biomass (kg)
10.2	51	1.76 ± 0.63	4.21 ± 0.81	11.72 ± 3.73	2.56 ± 0.64	1.85 ± 0.57	0.44 ± 0.20	16.91 ± 6.23	40.34 ± 7.72	2,864 ± 691	8.20 ± .36	2.14 ± 0.92	5.13 ± 1.04	2.96 ± 1.06	10.07 ± 3.19
13.2	58	3.29 ± 1.12	5.30 ± 0.18	28.81 ± 9.89	6.32 ± 1.93	3.34 ± 0.98	0.63 ± 0.24	33.05 ± 14.71	51.97 ± 3.77	4,168 ± 1,110	8.24 ± 1.10	1.27 ± 0.14	7.93 ± 1.99	2.40 ± 0.34	15.99 ± 1.26
16.2	63	3.89 ± 0.51	4.45 ± 0.91	29.75 ± 6.59	7.79 ± 0.20	5.14 ± 1.58	0.91 ± 0.26	34.89 ± 9.43	41.13 ± 16.58	3,880 ± 382	8.58 ± 1.33	1.56 ± 0.17	12.13 ± 1.39	2.53 ± 0.86	29.06 ± 3.83
19.2	67	3.37 ± 0.93	4.77 ± 0.86	27.59 ± 12.38	7.44 ± 2.95	3.88 ± 1.19	0.70 ± 0.12	30.38 ± 2.79	43.80 ± 4.15	3,651 ± 388	8.04 ± 0.89	0.96 ± 0.28	7.52 ± 4.86	1.82 ± 0.60	24.18 ± 15.60
22.2	71	4.78 ± 0.40	4.76 ± 1.64	40.76 ± 14.23	12.71 ± 8.67	6.03 ± 2.21	1.09 ± 0.39	51.25 ± 11.53	48.42 ± 6.72	4,649 ± 628	9.83 ± 0.92	1.15 ± 0.29	13.80 ± 8.94	2.15 ± 0.61	32.02 ± 18.21
25.2	75	5.73 ± 0.40	5.66 ± 1.73	57.10 ± 9.11	17.01 ± 4.04	8.69 ± 2.65	1.11 ± 0.49	41.64 ± 6.19	41.99 ± 16.51	4,680 ± 1,179	9.38 ± 1.67	1.61 ± 0.73	26.06 ± 7.90	3.40 ± 2.01	70.81 ± 14.25
28.2	77	3.18 ± 0.58	6.57 ± 0.83	34.19 ± 9.36	11.60 ± 1.15	4.56 ± 0.82	0.48 ± 0.06	26.99 ± 4.13	55.62 ± 1.26	2,896 ± 640	8.84 ± 1.47	1.27 ± 0.38	14.47 ± 3.10	3.29 ± 1.09	41.09 ± 11.47
34.2	81	4.13 ± 1.11	5.52 ± 0.07	38.59 ± 11.33	10.53 ± 2.97	4.94 ± 1.25	0.75 ± 0.20	32.62 ± 9.52	43.54 ± 3.03	3,207 ± 623	9.36 ± 0.31	1.42 ± 0.15	15.15 ± 5.08	3.02 ± 0.31	48.79 ± 11.45
43.2	86	5.00 ± 1.50	3.54 ± 0.23	34.75 ± 11.85	9.36 ± 6.41	5.85 ± 2.86	1.43 ± 0.49	54.43 ± 16.73	38.70 ± 4.90	4,125 ± 429	8.48 ± 1.48	1.74 ± 1.15	15.65 ± 10.90	2.51 ± 1.44	49.55 ± 32.90
55.2	90	4.13 ± 1.33	7.55 ± 0.82	50.38 ± 14.32	12.27 ± 5.41	4.70 ± 1.92	0.56 ± 0.22	32.31 ± 15.25	56.48 ± 6.24	3,014 ± 1,148	8.35 ± 1.66	2.27 ± 0.20	27.79 ± 11.69	5.91 ± 0.14	63.94 ± 26.53
88.2	94	5.44 ± 2.86	5.78 ± 0.87	56.12 ± 31.89	15.94 ± 11.0	7.22 ± 5.19	0.99 ± 0.61	41.06 ± 21.46	43.62 ± 6.66	3,483 ± 1,089	7.50 ± 0.58	1.84 ± 0.88	25.31 ± 10.39	4.04 ± 1.55	94.33 ± 49.59
Equation		-9.78 + 32.6*IR -18.21*IR ²	2.34 + 4.12*IR -0.19*IR ²	-82.06 + 251.32*IR -118.04*IR ²	-42.47 + 123.73*IR -68.67*IR ²	-19.63 + 60.74*IR -35.81*IR ²	-2.25 + 7.73*IR -4.68*IR ²	-98.06 + 336.48*IR -203.74*IR ²	20.47 + 63.90*IR -38.63*IR ²	-5,013.88 + 25,086.85*IR -17,474.34*IR ²	-5.59 + 40.5*IR -27.94*IR ²	-24.66*IR +17.41*IR ²	24.78*IR +15.23*IR ²	-11.35 + 13.19 -33.90*IR +26.58*IR ²	104,14*IR ^{3.2934}
Coefficient (R^2)		0.31	0.13	0.36	0.30	0.23	0.12	0.18	0.01	0.10	0.16	0.24	0.41	0.31	0.88
Significance		**	ns	**	**	**	ns	*	ns	ns	ns	**	**	**	**

**Significant at 1%, * significant at 5%, ns—non significance.

The foliage area of *E. camaldulensis* showed the same tendency to increase with solar radiation. Plants exposed to the highest available irradiation exhibited a foliage area about five times larger (25 m^2) than those exposed to half the amount of irradiance (5.13 m^2). Despite this great variation, leaf density remained stable around $1.5 \text{ m}^2 \cdot \text{m}^{-3}$ throughout the transect with very little increase toward the sunnier places. The leaf area index (LAI) increased with rising solar radiation. This difference was due to the canopy shape, which was slender near the shading trees but more round at a greater distance (values close to 1.0 at 94% IR). In contrast, specific leaf area ranged from 8 to $9 \text{ m}^2 \cdot \text{kg}^{-1}$ with a slight tendency to decrease on a gradient from shade to full sun exposure.

Total above ground biomass presented a steep augment with increasing available solar radiation as can be seen in Table 1. Trees receiving 51% IR presented only a tenth (10.07 kg) of the total dry biomass from those receiving 94% IR (94.3 kg). Half of the maximum biomass accumulation was achieved with about 80% IR.

Although tree height was increasing towards full sun exposure, no significance was found (data not shown) indicating that trees were not etiolated in reduced solar irradiation of up to 51% IR. Moreover, plants located under 51% IR had fewer sprouts per stump (a maximum of two) than those located farther away. Apart from visual impacts no significance was found in this characteristic. The percentage of the tree comprised by the canopy did not change significantly throughout the transect. Canopy height (average 5.3 m) as well trunk height (average 6.3 m) remained about the same, making up approximately 46% and 54% of the tree height, respectively.

Another way to analyse the data is to determine the relationship of values from each location on the shading transect with those of plants located farthest away from the shading trees – *i.e.* to those exposed to almost 100% IR and analyse them graphically as a function of available irradiance. At Figure 2, it is possible to visualise the straight relationships between irradiation fraction and canopy surface (2A), canopy volume (2B), total leaf area (2C) and canopy projection area (2D), with a steep increase of values towards full sun exposure for all characteristics.

DISCUSSION

It is important to point out that no separation on water and irradiation competition was performed once we arrived in the area years after initial growth. A long term research regarding this aspect can be done by inserting a plastic sheet in the soil between fields accordingly to the methodology proposed by Willey and Reddy (1981) and thus avoiding root competition. In our study, we were concerned to assess the canopy modifications due to changes in the above ground environment.

To our knowledge there is no study dealing directly with the effect of shade on eucalypt growth or adaptation to different radiation environments. Of the few research papers that study shading, most aimed to evaluate the production of seedlings. These papers indicate the necessity of high irradiance levels for the development of *Eucalyptus* even at this early stage. In Australia, Withers (1979) observed the death of all *E. ovata* seedlings when submitted to only 30% of available irradiance. Also, Doley (1979)

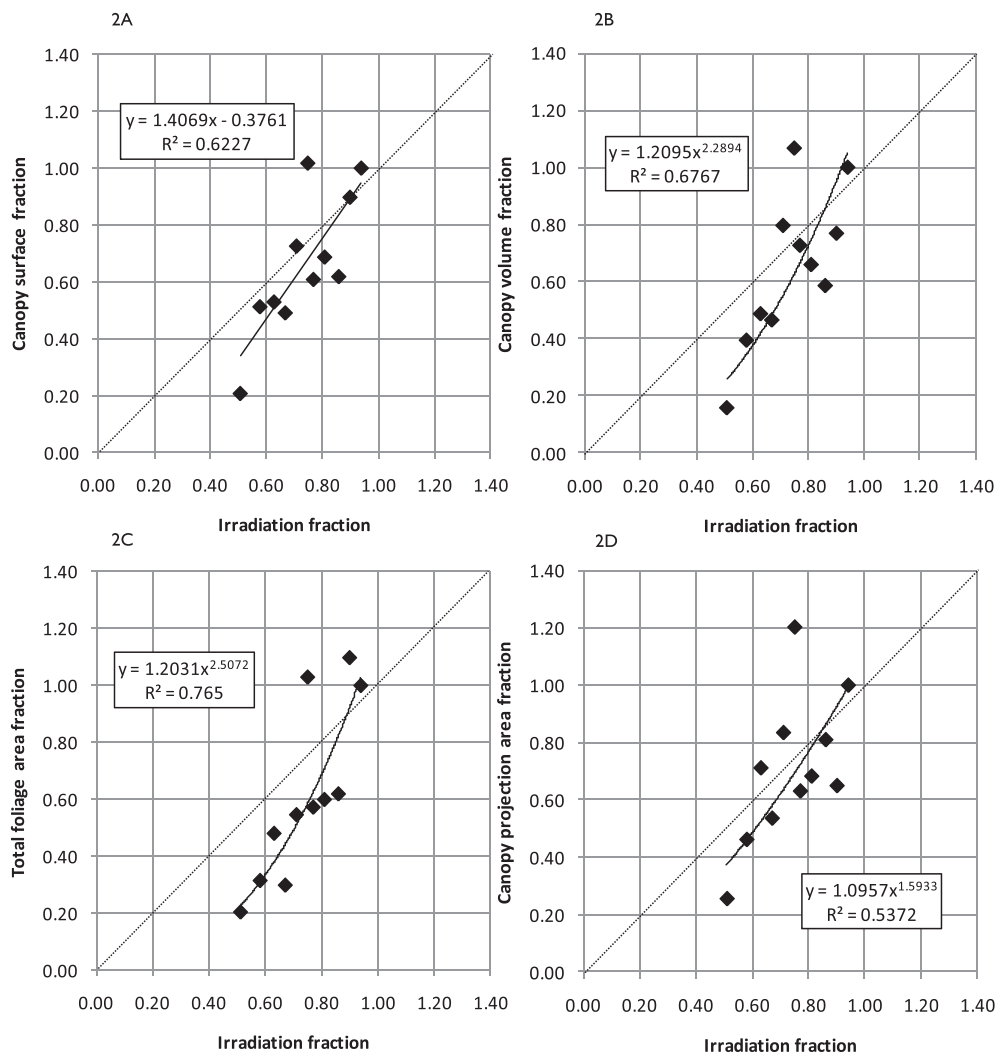


Figure 2. Relationship of irradiation fraction and the fractions (means values found in each shade location divided by those of plants located farthest away from the shading trees) of: canopy surface (2A) canopy volume (2B); total foliage area (2C) and; canopy projection area (2D) of *E. camaldulensis* sprouts planted at the Experimental Station of Forestry Science of Anhembi (ESFSA) - Department of Forestry Science of the Escola Superior de Agricultura “Luiz de Queiroz”, University of São Paulo (ESALQ/USP) in Anhembi-SP/Brazil (22°40'S, 48°10'W).

observed that cambial cell division decreased by 50% in *E. grandis* seedlings when submitted to shade (2.8 E m²·day⁻¹ for seven weeks).

In our study, the increase of values towards full sun exposure as shown in Figure 2 (A to D) contrasts the more stable values in Table 1. Other characteristics measured in *E. camaldulensis* sprouts did not follow this pattern: *i*) tree, trunk and canopy height show a slight tendency of increase towards full sun that was not significant; *ii*) canopy

opening and canopy percentage show no perceived direct relation to irradiation level as well as; *iii*) canopy projection and canopy rounding off.

Leaf density may be a conservative factor for *E. camaldulensis* as no significant tendency of increment was found in any direction (i.e. from 51 to 94% IR). A much denser canopy in plants exposed to high irradiation levels was expected. This is commonly found in many cultures such as coffee plants (Righi *et al.*, 2007) where canopies are twice as dense in monocrop cultures (full-sun) than plants cultivated in agroforestry under rubber trees receiving about half of the available sun irradiation. Denser canopies found in full-sun coffee plantations can be viewed as an adaptation, not only to capture more radiation, but also to protect plants from the high irradiance levels in the tropics. In *E. camaldulensis* (and probably in many other *Eucalyptus* species) leaf density was only about $1.5 \text{ m}^2 \cdot \text{m}^{-3}$. Coffee plants show a much higher value, with $21 \text{ m}^2 \cdot \text{m}^{-3}$ in plants receiving 50% IR and about $40 \text{ m}^2 \cdot \text{m}^{-3}$ in plants in full-sun monocrop (Righi *et al.* 2007). Binkley *et al.* (2010) found that larger *Eucalyptus* trees within a stand were able to grow more as they received more radiation and to use it more efficiently, producing more mass per unit of irradiance. The authors verified by a computational model that irradiance interception increased linearly (or even exponentially, Binkley *et al.*, 2013) with the increments of canopy foliage, with the relationship remaining roughly at the same level per unit of leaf area.

Leaf characteristics such as size, thickness, number of stomata, etc., play an important role in plant performance related to the species' strategy of resource acquisition and adaptation to a specific environment. These variables are widely used in crop science and community ecology studies (Vile *et al.*, 2005). Thicker leaves are sometimes associated with higher construction costs and with a longer lifetime than thinner ones (Mediavilla *et al.*, 2001). Wilson *et al.* (1999) pointed out that leaf-dry mass, a variable largely independent of leaf-thickness, would be much more useful as a predictor of its location on an axis of resource capture, usage and availability. However, to date SLA is the most commonly used trait (Westoby, 1998) as an indicator of plant adaptation to the environment.

The lack of leaf layers (displayed by low leaf density) of *E. camaldulensis* and the low variation of SLA (the higher the value, thinner the leaves) under contrasting conditions means that it can bear high irradiation levels. In fact, higher irradiation is required by this tree species. On the other hand, this low adaptability capacity means that *E. camaldulensis* needs very specific conditions to develop satisfactorily. The SLA values exhibited by *E. camaldulensis* ($8.6 \text{ m}^2 \cdot \text{kg}^{-1}$) are similar to those found in coffee plants in full sun. For the latter, values were twice as higher of those plants that submitted to about 50% IR (Righi *et al.*, 2007).

Quentin *et al.* (2011) found a compensatory response of transpiration rate and canopy conductance of partially defoliated *E. globulus*. The authors attributed this to an increase in water supply per unit of leaf area. Many authors have found photosynthetic up-regulation after defoliation of different plants (Fang *et al.*, 2006; Lavigne *et al.*, 2001; Pinkard *et al.*, 2007, etc.). However, a down-regulation is not commonly reported as: i) it is not of interest whether *Eucalyptus* is the main crop or ii) *Eucalyptus* has a very low

ability to decrease radiation and CO₂ compensation points, as indicated by the results of this study and those of Binkley *et al.* (2010) – need further investigation.

Stomatal conductance and thus photosynthesis vary linearly, both being directly affected by inner plant hydraulic resistance (Hubbard *et al.*, 2001; Meinzer and Grantz, 1990). *Eucalyptus* seems to have a very low inner hydraulic resistance and a high ability to maintain stomatal opening. At large scale vegetation stands, such as forests and woodlands, the vegetation structure may modify the leaf level control of water loss due to its strong coupling with the atmosphere. The transpiration control is therefore maintained at the canopy level (Roberts, 2000). The study of the responses of shaded *Eucalyptus* with regard to stomatal conductance, sap flow, photosynthesis, etc., offers ample opportunities for future research.

Leaf density and canopy architecture of tree species determine the fraction of solar energy that can be captured by plants of the lower strata (Monteith, 1965). Thus, the effects of shadowing on the physiology of species growing in mixed plantations are important in determining the optimum levels of temperature and radiation, since these are crucial for photosynthetic processes (Bernardes *et al.*, 2009). In this sense, the study of physiological responses to different levels of shading and tree-crop interactions can assist in determining optimal species composition and management of AFS (Baggio *et al.*, 1997; Cannell, 1976). Considering the age of sprouts and site conditions presented in this study, growing *E. camaldulensis* under shady conditions seems inadequate. Our results suggest an early planting strategy, to save time and to provide better environmental conditions at early developmental stages.

Direct measurement of leaf area is the most precise method and for this reason it is often used as a calibration tool. The leaf area index (LAI) depends on spacing, age and phenological phases (Jonckheere *et al.*, 2004). Also, site conditions and management practices can significantly alter plant responses to the environment as indicated by Righi and Bernardes (2008) in a study of rubber trees. LAI measurements can also be useful since they could relate phenological phase (Righi *et al.*, 2003) with the timing of field work, thus greatly improving the outcome of production and reducing labour costs in rubber plantations (Righi and Bernardes, 2008). LAI can be used to evaluate canopy dynamics in *Eucalyptus* since it is a consistent factor as identified by Chaves *et al.* (2007). The authors observed a high capacity of this tree to recuperate its canopy, reestablishing its architecture and radiation interception pattern after six months of pruning. In our study, total leaf area steadily increased towards full sun condition. Besides that LAI did not show the same tendency, since the area of canopy projection was not directly related to available irradiance.

A study by Minas Gerais, Brazil, Kruschewsky *et al.* (2007) observed a higher trunk volume of *Eucalyptus* only 38 months after planting in AFS, using wider spacing. These authors noted that productivity was more strongly affected by the number of trees per area than by the spatial arrangement of planting. Prasad *et al.* (2010) also found no significant differences in tree height and diameter at breast height (DBH) in different arrangements of 51 months old plants. In our study, we found a direct relation between trunk diameter and irradiance level (data not shown). Total dry biomass increased exponentially with rising available solar radiation. This contrasts

with the canopy saturation observed on coffee plants by Righi *et al.* (2007) with 50% IR. The few compensatory modifications on a canopy structure displayed by *E. camaldulensis* under lower irradiation levels were not enough to support similar dry mass accumulation as in full sun. The increments of leaf area with increasing irradiation lead to a higher irradiance interception (Binkley *et al.*, 2013) and use, resulting in a much higher biomass accumulation. It is important to observe that leaf density was almost unchanged (in any direction, from full sun to shade) and thus extinction irradiation coefficient remained unchanged within contrasting environment. In this way, photosynthesis per unit of leaf area would be the most important.

FINAL CONSIDERATIONS

A major task in developing production systems is the search for new silvicultural methods that consider the phenological development of natural forests. Also, it is necessary to consider requirements of developmental stages for different species and their interactions.

It seems that *E. camaldulensis*, and maybe many other *Eucalyptus* species, has a very low capacity to adapt, with few plastic characteristics. The thin canopy with low leaf density allows for great irradiation transmittance, indicated by the presence of well-developed understory on plantations with not so tight spacing.

It would be interesting to evaluate the growth of *Eucalyptus* (*many other species*) at early developmental stages to determine plant requirements. This would enable the development of artificial successional systems which could greatly increase farmers' revenues and also provide many environmental services.

CONCLUSIONS

E. camaldulensis showed little canopy plasticity under diverse irradiation conditions. Most of these variations were of small amplitude with some important variables remaining almost unchanged (leaf density, canopy percentage, tree, trunk and canopy height) or with only a small increase (leaf area index and canopy opening). Leaf morphology adaptation was very low, given the almost unchanged specific leaf area at contrasting radiance environments. The main variables that increased steeply towards full sun were: foliage area, canopy surface, canopy volume and area of canopy projection.

It is necessary to determine at which point the observed variations can sustain reasonable production so we can design appropriate agroforestry systems with young eucalypt growing under the shade of other crops.

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